THE LENGTH OF THE LIFE CYCLE OF A CLIMBING BAMBOO. A STRIKING CASE OF SEXUAL PERIODICITY IN CHUSQUEA ABIETIFOLIA GRISEB.*

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Certain plants are known to live vegetatively for many years, then flower and die. The most frequently cited example of this phenomenon is that of the century plant, *Agave americana*, which lives for a period of years without flowering, then sends up a tall, prominent inflorescence, and finally, after the maturing of the seeds, dies. This sexual periodicity is also characteristic of certain bamboos which blossom only after a cycle of years and then all simultaneously throughout an extensive region. The bamboos in the South Brazilian provinces of Santa Catharina and Rio Grande do Sul are said to blossom at intervals of about thirteen years, and *Bambusa arundinacea* on the west coast of Cisgangetic India blossoms at intervals of about thirty-two years (1). The complete and simultaneous dying off of the bamboos may in some communities prove disastrous by the wiping out of the chief available source of building material through the transformation of luxuriant bamboo forests into barren areas; or, it may prove of great economic value as a source of grain, especially when it comes, as it is said to (2), in times of drought and consequent famine.

The length of the interval of years varies greatly in different bamboos. Bean (3) reports that *"Bambusa tesselata* has been in cultivation for probably over sixty years, yet I have seen no record of its having flowered anywhere."* In striking contrast with this is the case of *Arundinaria falcata* var. *glomerata* which flowers almost every year on a certain number of culms. The latter is a case of partial or sporadic flowering as contrasted with the complete and simultaneous flowering which is the rule among bamboos. Intermediate types also exist. Bean (3) mentions the case of *Arundinaria Simoni* which flowered on odd culms in the bamboo garden at Kew for several years. He says, "excepting that the flowering culms died, the plants were in no way affected. . . . They continued to flower in this way every year up to 1903, by which time we had almost come to regard *A. Simoni* as a perennial. In that year, however, the plants flowered on every culm, and, after producing an abundance of seed, died. After that

not a single trace of leaf growth was ever visible and the plants were ultimately uprooted."

This peculiar periodicity in the life of bamboos was strikingly brough to my attention during a recent stay in Jamaica. On my first walk alon, the trail which runs from Cinchona to Morce's Gap in the Blue Mountains. my attention was called, by Dr. Duncan S. Johnson, to the many dead patches of the climbing bamboo, *Chusquea abietifolia*. Dr. Johnson re-
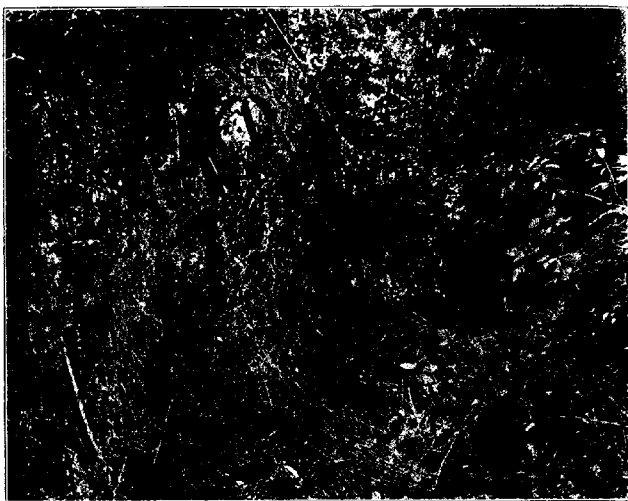

FIG. 1. An entanglement of dead *Chusquea abietifolia*.

marked that on three previous visits to Cinchona he had always found the Chusquea in full foliage, forming large entanglements which, like the tree ferns, stood out as a prominent feature of the tropical vegetation. The Chusquea was still there, interwoven into mats beside the mountain path or hanging in festoons above the trail, but the color was no longer green, for every plant seen on that first walk was dead. It was immediately suspected that this climbing bamboo had, true to the habits of its tribe, died as a result of profuse flowering following a long period of sexual inactivity. It seemed, therefore, advisable to collect all obtainable data bearing upon the life history of this Chusquea. These data here published will bring up to date the story of the life of the Jamaican Chusquea which was begun by Sir Joseph Hooker and Sir Daniel Morris thirty-three years ago. The present observations seem to fix the length of the life cycle.

The climbing bamboo, *Chusquea abietifolia*, is, in reality, a scrambler with no specialized climbing organs—although one's first encounter with the plant is likely to suggest the presence of vicious thorns, for the leaf midrib terminates in a very sharp, protruding point. The long, erect young shoots push upward among the surrounding plants and are held from slipping back by the subsequent development of whorls of leaves and lateral branches. The height attained seldom exceeds 30 feet, while the mats of interwoven stems are often 10 to 15 feet across. If high supports are lacking Chusquea succeeds very well in climbing over low shrubs. The maximum basal diameter of the old culms is hardly a quarter of an inch, in contrast to the 5- and 6-inch culms of the closely related *Bambos (Bambusa) vulgaris* of the Jamaican lowlands.

Chusquea abietifolia is little known outside of Jamaica. It has been reported (4) from only two other localities, both in the West Indies—

FIG. 2. Growing seedlings of *Chusquea abietifolia*.

Porto Rico (Monte Alegrillo) and Haiti (Monte Furcy). In Jamaica this rare bamboo is confined to the mountainous interior of the island. It does not occur much below 4,000 feet and is most abundant on the mountain ridges, being found on the very summit of Blue Mountain Peak, 7,360 feet above sea level.

The habitat of the plant is apparently not so definitely dependent on moisture as it is on altitude, although the lower limit of 4,000 feet is

possibly fixed by moisture requirements. Rainfall in the higher altitudes of these tropical mountains is always ample for vegetation, yet there is a pronounced difference in the soil moisture of exposed ridges and shaded ravines. Chusquea is found in both these regions; on the sunny, hot, dry spurs where vegetation is relatively sparse, and in the dark, cool, wet gulches where tree ferns and other moisture-loving plants abound. Chusquea is, however, most abundant under conditions intermediate between these two.

Published descriptions of this climbing bamboo are few and brief, that of Grisebach, in his *Flora of the British West Indies*, being among the earliest. A more complete systematic account by J. D. Hooker appears in the *Botanical Magazine* (Curtis) for 1885. The first definite reference to sexual periodicity in Chusquea appears in a short notice by Morris in the *Gardener's Chronicle* for 1886. He writes, "The flowering of this plant appears to take place, as in most Bambuseae, at long intervals."

The data pertaining to the life habits of *Chusquea abietifolia* published here were obtained from the following sources: first, from Wm. Harris, government botanist of Jamaica, to whom I am greatly indebted for many kindnesses during my stay on the island: second, from several published articles herein referred to, which were kindly brought to my attention by Assistant Director Arthur W. Hill, of the Royal Botanic Gardens at Kew: third, from the notes of Daniel Morris and J. H. Hart recorded in a copy of Grisebach in the library of Hope Gardens, Jamaica: fourth, from the natives living in the mountains, especially David Watt, whose long experience in collecting for Jamaican and visiting botanists has made him uncommonly familiar with the plants of the mountain forests: and lastly, from my own observations covering a period of six weeks and extending over a ten-mile stretch of the Blue Mountain Range.

During June, 1919, nearly all mature plants of *Chusquea abietifolia* in the Blue Mountains of Jamaica were dead. On the other hand, the ground in many places was covered with seedlings varying from an inch to 18 inches in length. Diligent search brought to light only a few patches of old, living plants. Still fewer specimens were found bearing fruit.

The first question which naturally arose was, when did this climbing bamboo last flower? I was informed that there had just ended a most profuse flowering of all plants in the mountains wherever seen, and that the time of flowering extended over more than a year. The question which next presented itself was, how long a time had elapsed between this and the last previous flowering? Definite information on this point was obtained from Mr. Harris, who writes, "Chusquea flowered generally in the Blue Mountain regions in 1885-6 and died down everywhere." This first recorded flowering period also extended over more than a year, as is evident from the note of Hart supplementing that of Morris. The latter states that Chusquea was first noticed in flower in the fall of 1884, and that in

1885 it flowered generally. Hart adds, "It flowered also in 1886 or rather continued flowering from 1885."

That the outcome of the recent flowering of Chusquea—the death of all mature plants and their replacement by innumerable seedlings—is identical with that following the last general flowering 33 years ago, is evident
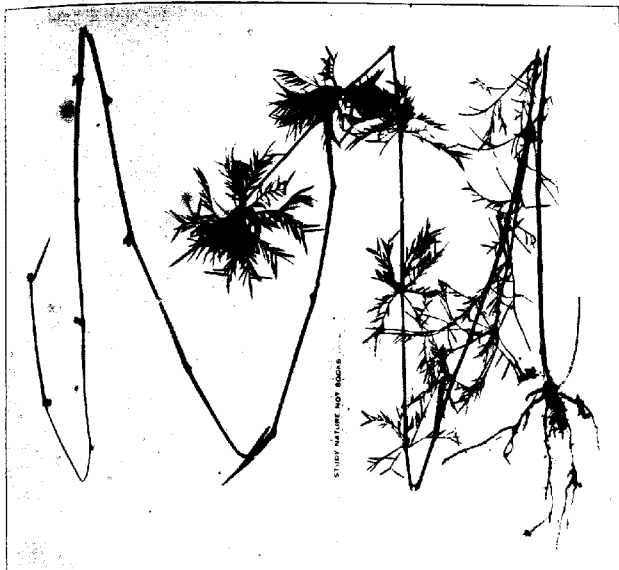

FIG. 3.   An old basal culm of *Chusquea abietifolia* with a long, young, leafless shoot.

from the writings of the early observers.   Morris (5) tells the story in this manner:' The Chusquea "began to shed its leaves and to assume a dull, rusty color. . . .   When the seed was set the stem began to die down, and apparently every plant in the island died, root and all.   At the present time (1886) the ground in the forests where the Chusquea grew is covered with millions of seedlings, and in due time these will take the place of the former generation."

In 1884 some plants of Chusquea were sent in a Wardian case to the Royal Botanic Gardens at Kew.   Hooker, referring to the Kew plants, wrote: "In December last (1884) they suddenly burst into flower causing me to fear that, after the manner of so many species of this most remarkable tribe of grasses to which they belong, they may not survive the flowering

period." The Kew plants died just as did the wild ones. It is worthy of special note that the Kew plants, after being transplanted to an entirely new and different environment, flowered simultaneously with the wild plants in Jamaica.

It is, therefore, immediately apparent that *Chusquea abietifolia* had just ended (in 1918) a life cycle of about thirty-three years during which time it had grown vegetatively only, until the last year when it flowered, disseminated its seeds, and died.

There are but three other species of climbing bamboo, all belonging to the genus Arthrostylidium. These also, like the Jamaican Chusquea, are found only in the West Indies. It is very probable that at least one of these other species goes through a cycle similar to that of *Chusquea abietifolia*. *Arthrostylidium sarmentosum* has been collected in flower only once (6).

Many days of tramping over the mountain trails near Cinchona revealed but a single green specimen of Chusquea, the only living plant among many hundreds of dead ones bordering the trail in the two-mile walk from Cinchona to Morce's Gap. Whether the presence of this sole living mature plant among so many dead ones is due to certain edaphic conditions which have delayed flowering and thus possibly produced a plant of altered life cycle, is uncertain. Its possibility will be discussed in detail later.

The ascent of Blue Mountain Peak showed a similar state of affairs to exist in that locality. The trail to the summit was lined with innumerable patches of dead bamboo. Several green plants were found but these few were not fresh and thriving in appearance, being apparently in a dying condition.

Some days later I learned of green plants growing on an exposed, rocky spur. Investigation first revealed short, fresh, green tufts of Chusquea, which proved to be young shoots from old rootstocks. This region had recently been burnt over. The charred stubble was still evident. The presence of green Chusquea here seemed easily explainable: the parent plants had been burnt to the ground before their life cycle was complete, and the living rootstocks had sent up new shoots which were continuing the growth of the plants and thus carrying on the vegetative portion of the life cycle beyond the normal limit. Opposed to this supposition is the statement of Hackel (7) that small plants from cuttings or layers of bamboos blossom at the same time as do the parents from which they were taken. It would be very interesting to determine experimentally just how such a catastrophe as the destruction of that part of the plants above ground shortly before their time of flowering would affect the normal life history of a plant like Chusquea.

Continuing along the spur above mentioned, I subsequently found a fair-sized area with numerous old but green and thriving plants. They were not in flower but were healthy, actively growing specimens, sending out an abundance of long, young shoots. Here was a prominent exception

. . the general condition existing throughout the mountains. A noteworthy
.ture of the exception, however, was the fact that these healthy, green
. nts were all in a single and comparatively small area. The possibility
. explaining their persistence by some external cause is, therefore, greater
. .n would be the case had several distinct scattered groups been found.

The region in which these living plants are growing is one experiencing
.e extreme of mountain aridity above 4,000 feet. The ridge is hot and dry,

FIG. 4. Seedlings of *Chusquea abietifolia*.

and covered with vegetation characteristically xerophytic (*Pteris aquilina,
Gleichenia Mathewsii, Agave americana*). Morce's Gap trail and Blue
Mountain Peak; on the other hand, where Chusquea is, with few exceptions,
to be found only as old, dead plants and young seedlings, are moist regions
characterized by hygrophilous plants. Immediately below the dry area
where the patch of living bamboos exists, there is a moist, shaded gulch
where no living, mature Chusquea was found; for here, in an environment
like that at Morce's Gap and on Blue Mountain Peak, the old bamboos are
dead and seedlings are abundant. . Here also flourishes a hygrophilous
flora of tree ferns and succulent herbs. It seems, therefore, reasonable to
conclude that the climbing bamboo has in this more arid region in some man-
ner assumed an altered life cycle. The single green specimen, already
referred to, found near Morce's Gap was growing on the hot and dry south-
west slope of the mountain, a spot differing markedly from the nearby,
shaded, semi-moist regions along the trail where Chusquea was represented
by an abundance of dead plants and of living seedlings.

One rather welcomes an exception to the striking regularity in sexual periodicity of a species extending over a large territory. Indeed, one would expect not a single exception but many, brought about by different rates in seed germination, and in growth both of seedlings and mature plants due to differences in environmental factors such as moisture, light, temperature, and soil, which would ultimately give rise to plants whose time of flowering would precede or follow that of the majority, and which would thus, in time, produce many plants whose life cycles overlapped so that some out of the many could be found in flower in any year. It would be exceedingly interesting to attempt to bring about such a state artificially by deferring the sowing of the seed, and thus attempting to postpone the time of flowering or to shorten the life cycle. It would seem, however, that this experiment must have been many times performed by nature (*i.e.*, if the seed is capable of germinating after 1 or more years) so that we should be able to judge from the present condition of the wild plants of Chusquea whether the cycle can be altered in this way. Bean (3) is of the opinion that the simultaneous flowering of bamboos follows some general law. What this general law might be he does not suggest. Yet he does believe that under cultivation the system of simultaneous flowering of some of these species would appear to be breaking down, and he cites the case of *Arundinaria Falconeri* which flowered in England, in the vast majority of cases, in 1876, but the flowering of the generation at the time he wrote (1907) had already extended over five seasons. That a breaking down of simultaneous flowering in *Chusquea abietifolia* is taking place in the wild state is suggested by the exceptions that I have noted and by the fact that this climbing bamboo was detected in flower in 1911 and was also flowering freely at the base of Catherine's Peak, but not elsewhere, in November, 1912. In fact, Mr. Harris suggests, "It is just possible that individual plants of Chusquea may be found in flower in any year if careful search were made for them."

In spite of these several exceptions, it remains a striking fact that fully 98 percent of all plants of *Chusquea abietifolia* found in Jamaica in a region some ten miles in length, varying from 4,000 to 7,000 feet in altitude, and showing considerable diversities of light, temperature, and moisture, have flowered and died in a single brief period not exceeding two years, after a purely vegetative growth of more than thirty-one years.

This complete cycle of thirty-three years differs by only one year from that given by Brandis (8) for *Bambusa arundinacea* in India. It seems quite possible that the life cycles of these two genera are the same, for the exact time of flowering is not always readily determined. The general flowering of a species in one particular year may be heralded by a few forerunners the previous year and followed by that of laggards the next. Morris states that the last previous flowering of Chusquea in the Blue Mountains of Jamaica commenced in 1884, and Hart reports it as continuing until 1886. The exact time of the recent flowering is not definitely known.

...vid Watt is of the opinion that he first saw Chusquea in flower in the fall
1917.   I myself collected a few fruiting branches in the early summer of
19.   The climbing bamboo was, therefore, probably at the height of its
wering period in 1885 and in 1918, making the cycle one of thirty-three
ars.

I have referred to the possible effect of environment on change in time
flowering.   Equally interesting, and possibly as difficult of solution, is

FIG. 5.   Fruits of *Chusquea abietifolia*.   Collector, William Harris.

the ultimate cause of the simultaneous flowering of nearly all plants in a
certain locality.   The obvious suggestion, often made in such cases, that
this peculiarity is innate, does not, of course, solve the problem.   It simply
indicates that we must seek our explanation in causes operative before the
initiation of the individual.

Attempts to associate the sexual periodicity of plants with seasonal or

other environmental changes may seem as far-fetched as to ascribe to climate or food the periodic appearance of the seventeen-year locust which has this year (1919) infested certain regions of our country. It is however, quite possible that the duration of the life cycle of plants exhibiting sexual periodicity is the direct result of certain known, present or past, stimuli. An apparently very clear example of such an association between season and periodicity is seen in the life cycle of annuals which flower and die at definite seasons of the year. But one can not always be certain that the most evident and seemingly controlling factor in such a case is the one at present active. A native annual in the temperate zone commonly rests in winter, germinates in the spring, fruits in summer, and dies in the fall. This sequence of events one is likely to attribute to the sequence of the seasons. Yet most annuals if grown in a greenhouse where seasonal changes are non-existent (except as to light) can, by sowing of seeds at the proper time, be made to fruit in any chosen month of the year without regard to seasonal conditions out of doors. Thus are the successive steps, from germination to death, in the life span of an annual grown in a greenhouse accurately maintained without evident relation to any external controlling factor. That is, the annual germinates, fruits, and dies in the same interval of time that it always has required, and does this in an environment quite different from the seasonally progressive one of its natural habitat. This behavior seems clearly to belie the validity of the assumption that the present seasonal round determines the duration of each phase of the developmental cycle, and thus of the cycle as a whole.

There are reported, however, examples of the flowering of plants being regularly brought on by such external factors as moisture. The following is such an example cited by Morris (5): "A prolonged drought in India is often accompanied by the flowering of the common bamboo, and on this account the natives associate the two phenomena in a manner which is emphasized by the fact that the bamboo grain during seasons of drought has provided them with the only available means of support.". According to Ridley (cited by Schimper, 1) two species of Hopea and four species of Shorea blossom with great regularity every sixth year. These cycles are said to coincide with dry years. Morris (5) believes that the long intervals at which the flowering of Chusquea takes place probably depend "for their exact length upon the aspect of the prevailing seasons." Weather reports from Cinchona show, during the years preceding the recent flowering of Chusquea, no pronounced digression in temperature from the general average. The rainfall was unusually heavy for two years immediately preceding the flowering of Chusquea. It is hardly likely, though possible, that an over-abundance of rain should bring on a flowering period in Chusquea in Jamaica and drought be the cause of flowering of another bamboo in India.

Further proof against the theory that time of flowering is determined by

...ent seasonal factors is to be had from the behavior of the climbing bam-
... s sent to Kew. Morris (5) himself presents a bit of evidence against
... own contention when he says, "Both the wild plants at Jamaica and the
... tivated plants at Kew (although the latter were under such very different
... ditions) were in flower at the same time."

Should the life cycle of *Chusquea abietifolia* prove not to vary from the
...irty-three years which it has been found to be—just as the cycle of
:ambusa arundinacea has, from three successive observations (1804, 1836,
..868) been found to be exactly thirty-two years (1)—then it would seem
...ardly likely that the length of this term of years could be definitely ascribed
... present climatic influences, unless there is some larger climatic round
... years, such as that suggested by Brückner (9).

It is interesting to note, though of how much significance this may be
... pure conjecture, that the climatic oscillation ascertained by Brückner
.9) closely approaches in length of years the life cycle of Chusquea. There
... s, however, in addition to Brückner's 35-year alternation of wet and dry
...pochs, a supposed variation of rainfall in a cycle of eleven years, coinci-
...ently with the sunspot cycle (10). It is as yet by no means well established
that climatic changes are periodic, and there is but little to support the idea
that droughts occur rhythmically, especially with any great precision.

In considering the possible relationship between sexual periodicity in
plants and climatic oscillations I have had in mind—as I assume others
...ave had in their attempts to associate the two—only present climatic
...nfluences. That past rhythmical variations in rainfall or in temperature
...ave, through the ages, fixed the life-cycle of Chusquea is quite possible.
So striking is the association between the life of an annual and the seasons
that it seems very probable indeed that the cycle of annuals is the direct
...esult of seasonal influences, and that this cycle has, through many gener-
...tions, become so firmly established as to be unalterable through the tem-
porary elimination of seasons by transferring the annual to a greenhouse.

This problem can, however, and should, be attacked from other view-
...points than the purely ecological one. Other factors than such external
...timuli as droughts and similar seasonal epochs may have been at work in
...stablishing, or still are at work in maintaining, sexual periodicity in Chus-
...quea. The problem may be of the same nature as that of puberty and
...enility in organisms. We know, for example, that certain organisms re-
...quire a certain number of years in which to reach sexual maturity, and we
...now that certain organisms live about so long and never exceed a certain
...naximum. The present causes of such phenomena are not as yet seriously
...hought to be environmental in nature. That they may be somewhat in-
...luenced by environment is possible. Lack of food, for example, is said to
...asten the attaining of sexual maturity in man, but the digression from the
...nean is slight and has no direct bearing on the original establishment of
...he phenomenon.

In one respect, however, the periodicity of Chusquea differs strik¡ ¡gly from the cycle of annuals and the aging of organisms. That the span of life of an individual Chusquea is thirty-three years is no more remarkable and is as satisfactorily explainable as is the fact that an annual lives one year, man eighty years, and a Sequoia 5,000 years. But an hypothesis which will explain these phenomena is not necessarily sufficient to account for the simultaneous flowering of fully 98 percent of the individuals of a species extending over a great stretch of country.

There is as yet, it seems to me, no adequate explanation of the behavior of Chusquea. That seasonal factors at present active bring on this simultaneous flowering is very unlikely. That past climatic influences are responsible is quite possible. But the ultimate cause I should be inclined to search for in the physical and chemical make-up of its protoplasm; fully realizing, however, the possibility, indeed the probability, that this very nature of the protoplasm has come to be what it is in part because of its past environment as well as because of its own original constitution.

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SEX INTERGRADATION IN THE FLOWERS OF MERCURIALIS ANNUA

CECIL YAMPOLSKY

The older observers have repeatedly called attention to various aberrancies in plant structures, and these have been grouped under teratological phenomena. In this general category have been placed many unrelated phenomena as well as unexplainable ones. That has been particularly true with such occurrences as the appearance, upon a part of a plant which normally bore the organs of one sex, of the sex organs of opposite character. In another paper (1919) I have called attention to the fact that we may consider conditions such as the appearance of female flowers or branches on a male plant, male flowers or branches on a female plant, etc., as evidences of sex intergradation by no means uncommon in the plant kingdom.

In continuing my studies on *Mercurialis annua*, especially on the so-called monoecious form, I have observed some very interesting phenomena which appear to shed further light upon the question of sex determination. *Mercurialis annua* is described as appearing in three forms, male, female, and monoecious. The flowers of the female are, as a rule, two-carpeled, although often three-carpeled, and they are borne in clusters in the axils of the leaves. The flowers of the male are borne in interrupted spikes which surpass the leaves. The flowers of the so-called monoecious form (male, female, and hermaphroditic flowers) are borne like those of the female in clusters in the axils of the leaves.

The individual flowers of the three forms are minute and almost inconspicuous. The female flowers are apetalous, green—each carpel with a single ovule—a two-parted stigma which is white, translucent, and with roughened surface. In the instances in which there is either only one carpel or more than two, the stigma is undivided or multipartite depending upon the number of carpels. The carpels have a rough appearance due to the presence of characteristic translucent hairs. There are also two nectaries. The male flowers are apetalous with 8 to 20 stamens. Each stamen consists of a two-sacked yellow anther and a slender filament. The hermaphroditic flowers are like the female flowers with stamens borne from the bases of the carpels.

In a preceding paper (1919) I have reported upon the appearance of sporadic male flowers upon the female plants and of female flowers upon the male plants. Upon the female plants I have also noted and described various kinds of hermaphroditic flowers. Such flowers have also been observed on the so-called monoecious form but in much greater numbers.

Figures 1 to 7 of Plate V show a few of the forms that I have found. Figure 1 is a diagrammatic representation of a two-carpeled female flower showing (s) stigma, (n) nectary, and (t) hair. The appearance of the stigma and the hairs is particularly characteristic of the flower. Figure 7 is a diagrammatic representation of a male flower with several stamens, the dotted areas representing the anther sacs. In the female flowers there is never any evidence of an aborted or rudimentary stamen, nor is there any evidence in the male flower of an aborted or rudimentary pistil. Figure 2 is a diagrammatic representation of a very common type of hermaphroditic flower. The female elements are in all respects like those in the female flower. The male elements, the stamens, may arise at any point from the base of the carpel. The pollen grains are viable, and under favorable conditions self-pollination occurs and seed is set. In the light of what follows we may assume that the flower represented by figure 1 is more female than the flower represented by figure 2, in which the addition of a single stamen has added a characteristic of the male flower. Figure 3 shows a condition that is also quite common, an hermaphroditic flower with two stamens. These hermaphroditic flowers, too, are self-fertile, and seed is readily set. These flowers may be considered less female than the flowers represented by figures 1 and 2, inasmuch as there is an increase in the male elements. Figure 4 represents a condition in which more than two stamens occur together with the female elements. The number of stamens varies from three to sometimes more than eight. I have found many such flowers which have not been figured. Without sacrificing the functioning power of either the pollen grains or the ovules, various gradations in the proportion of male to female elements are produced in the hermaphroditic flowers. In figure 5 we have a condition in which the male elements have been substituted for half of the female elements. Figure 5 represents a flower with a single carpel, the other half of the flower being occupied by stamens. The number of stamens varies from 4 to 8. This arrangement differs from any described above because there has been a reduction in the amount of the female element so that, at best, the proportion of male and female elements is equal. In this condition, as in the preceding ones, there is no loss in the ability of the pollen or of the ovule to function either in self- or cross-pollination. Figure 6 shows a flower very similar to the one represented in figure 5 but with the addition of one or more stamens arising from the base of the single carpel. In this instance the male elements overbalance the female and the flower is decidedly more male than female. With the male and female flowers as the extremes of a series I have found, in my female and so-called monoecious cultures, intergrading flowers that suggest intergrading degrees of maleness and femaleness. It is interesting to note that this intergradation is not accompanied by sterility as is the case in the transition of ovaries into testes and testes into ovaries in the reported cases in animals.

In the three-carpeled flower I have not found the diversity of intergradation that I have described for the two-carpeled flower. Many of these three-carpeled flowers have been observed with a single stamen, some with two stamens, with three stamens, and with six stamens. The pollen when examined appeared to be perfectly healthy and normal.

While continuing the observations on the above described conditions within the flowers of the so-called monoecious form, an even more striking intergradation of parts, namely pistillody of the stamens and staminody of the pistils, was noted. There were hundreds of flowers that showed such a condition.

Botanical literature abounds with many illustrations of the transmutation of pistils into stamens and of stamens into pistils. The texts on teratology give many illustrations. Without going further into the literature on this subject, I wish to cite the work of Haring (1894). He gives an elaborate series of drawings showing various transition stages of stamens into pistils and of pistils into stamens in *Salix caprea* L. and *Salix cinerea* L. To Haring this facility with which one sex organ is transmuted into another is an indication of the morphological equivalence of sex organs of the opposite sexes.

In the flowers of Mercurialis under observation, most elaborate and varied transition stages appeared of stamens into pistils and of pistils into stamens. Because of the minuteness of the flower, the flower buds were removed and examined under a binocular microscope. Figure 8 represents a female flower with an anther sac growing from one side. As far as could be determined, the ovaries were normal. The pollen grains were for the most part plump and appeared healthy. Figures 9 and 10 are parts of a single three-carpeled hermaphroditic flower. The carpels appeared to be normal; the stamens showed transition stages into pistils. In one stamen (fig. 10) there was one anther sac, in a second one (fig. 9) one of the anther sacs was much reduced in size. There can be no doubt that these stamens had been partially transformed into female tissue, because they showed the white translucent stigmatic surface and the hairs, characteristic of the female flower. The anther sacs were yellow like those of the normal stamens. The pollen from each of the anthers appeared healthy.

Figures 11, 12, and 13 are parts of a two-carpeled hermaphroditic flower with what appear to be two anthers. Figure 11 is evidently a transmuted stamen, showing the stigmatic tissue and the hairs of the female flower. There was no trace of an anther sac or of an ovary. It was completely sterile. The second stamen (fig. 13) had the characteristics of both the stamen and the pistil. It had two anther sacs of unequal size and the stigmatic character and hairs of the pistillate part of the flower. One of the carpels (fig. 12) had imbedded within its tissue an anther sac. The majority of the pollen grains in this sac were plump and appeared normal. This flower, then, showed both staminody of the pistils and pistillody of the stamens in a very marked degree.

Figures 15 to 19 are of a single three-carpeled hermaphroditic flower with four stamens. In only one of the stamens (fig. 15) was there an anther sac. The pollen grains were for the most part plump and appeared healthy. The other three anthers (figs. 16, 17, 18) looked externally like individual carpels although internally there was no evidence of differentiation into fertile and sterile tissue. The three carpels (fig. 19) contained differentiated ovules somewhat enlarged in size and they had an appearance that suggested oedema.

Figures 20 to 22 represent parts of a three-carpeled female flower almost entirely transmuted into stamens. The fact that the flower contained only three parts is evidence that it is a three-carpeled female flower and not a reduced male flower. The pollen grains from each of the sacs showed few shriveled grains.

The male flowers show an equally strong tendency to grade into the female through a series of gradations, from the faintest suggestion of a stigma to the presence of an ovary and of an apparently normal ovule. Figure 24 shows a male flower with ten stamens, two of which have been partially transformed into female tissue, each bearing one anther sac. The remaining eight stamens are normal. Most of the pollen grains in the sacs of the transmuted stamens were normal in appearance.

Figures 25 to 30 represent parts of a single male flower, seven of which were normal, the rest in various stages of transformation. Figure 30 is a normal stamen. Figure 27 represents a stamen with an indication of a stigma, the tissue being white and translucent. The stamen in figure 25 is a little more female, while figures 26 and 29 show more extreme conditions of femaleness. Figure 28 shows a combination of male and female elements, a fully developed stamen and a carpel with a well-developed ovule.

Figure 14 is a part of a male flower much like the one described above, but in which only two stamens were abnormal. The stamen represented by figure 14 had a completely developed ovary (o) and two large anther sacs with apparently healthy pollen.

Figure 23 shows a stamen with four anther sacs and a completely developed ovary. This was taken from a flower otherwise male.

It is impossible here to give the numberless variations that occurred in all three kinds of flowers. The illustrations cited give an idea of what is occurring. This evidence of pistillody of the stamens and of staminody of the pistils, coupled with the apparently normal arrangements of male and female elements as seen in figures 1 to 7, emphasize all the more strongly that intergradations within the flowers may occur by steps that are almost insensible. With the female flower as one extreme and the male flower as the other, flowers may grade all the way toward femaleness from the male extreme and all the way toward maleness from the female extreme.

While it has not yet been determined whether or not intergradation is here accompanied by sterility, the indications from the appearance of the

...llen and the ovules suggest that total sterility does not occur. Gold-
...hmidt (1916), in his crosses between European and Japanese races of the
...psy moth, *Lymantria dispar*, secured individuals that showed gradations
... maleness and femaleness. Such a condition was usually accompanied
...y sterility. Banta (1916, 1918) finds that in his Crustaceans the more
...ronounced the sex intergradation the more sterile the form became.
While a flower of a plant may not be compared to an individual like a moth
or a Crustacean, it is interesting to note that in plants sex intergradation
is not, as a rule, accompanied by sterility. On the contrary, the plants
whose flowers were studied showed no diminution in seed production or in
general vigor.

The condition of intergradation within a series of flowers on a single
plant brings up interesting considerations bearing upon the question of
when and how the sex of each flower is determined. The *Anlagen* or deter-
miners, if there be such, must be different for the different flowers according
to the arrangement of their parts. It must be borne in mind that in this
so-called monoecious form of Mercurialis the sex of the plant changes in
the course of the plant's development. The initial flowers are female.
Several weeks after germination the young plant produces female flowers,
and only female flowers are produced for several months. Then a few
male flowers or hermaphroditic flowers appear. These increase in number
as the season advances. As far as the whole plant is concerned, there is
a periodic alteration of sex. A factorial hypothesis for sex cannot explain
these results. It would seem logical to assume that the sex of the flower is
determined at the time of its formation and not when the plant of which
it is a part is in the fertilized egg stage. Moreover what seems to hold true
for such flowers as represented in figure 1 to 7 apparently does not hold for
the aberrant conditions I have noted. In the various transitional forms
there seems to be no definite factor which determines the sex of the flower;
pistil passes into stamen and stamen into pistil at any time in its develop-
ment. The argument for strict sex segregation is obviously nullified because
of the behavior of these forms. The line of demarcation between what is
male and what is female is wavering and vague. The evidence brought
out here tends to emphasize an epigenetic condition for sex rather than the
presence of definitely localized qualitative or quantitative factors.

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EXPLANATION OF PLATE V

FIG. 1. Female flower: (s) stigma, (n) nectary, (t) hairs.

FIG. 2. Hermaphroditic flower with one stamen.

FIG. 3. Hermaphroditic flower with two stamens.

FIG. 4. Hermaphroditic flower with more than two stamens.

FIG. 5. Hermaphroditic flower with single carpel, the other half occupied by stamens.

FIG. 6. Hermaphroditic flower with single carpel, the other half occupied by stamens, also two stamens from the base of the single carpel.

FIG. 7. Male flower.

FIG. 8. Female flower with a single anther sac without filament budding out of the side of a carpel.

FIGS. 9–10. Parts of a three-carpeled hermaphroditic flower, the three stamens showing transitional stages.

FIGS. 11–13. Parts of a two-carpeled hermaphroditic flower. FIG. 11. Stamen completely changed into sterile tissue with female characteristics. FIG. 12. Anther sac imbedded within the tissue of one carpel.

FIG. 14. Part of a male flower having anther sacs and (o) ovule.

FIGS. 15–19. Parts of a three-carpeled hermaphroditic flower. Figs. 15–18. Transformed stamens: (as) anther sacs.

FIGS. 20–22. Parts of a three-carpeled female flower transformed into stamens.

FIG. 23. Stamen with four anther sacs and a single ovule (o).

FIG. 24. Male flower with two stamens in transitional stages.

FIGS. 25–30. Parts of a male flower in various transitional stages: (o) ovule, (ns) normal stamen.
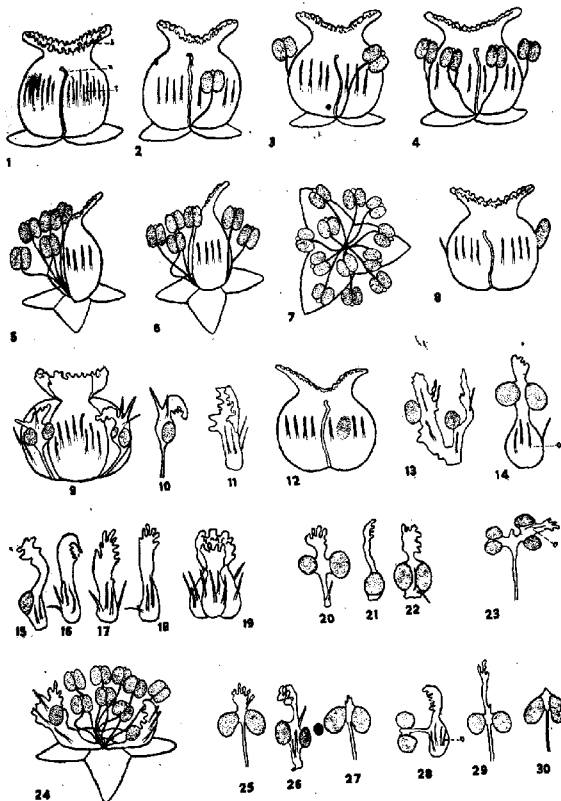
YAMPOLSKY: SEX INTERGRADATION IN MERCURIALIS ANNUA.

THE UPWARD TRANSLOCATION OF FOODS IN WOODY PLANTS. I. TISSUES CONCERNED IN TRANSLOCATION

OTIS F. CURTIS

It seems to be very generally believed that in shrubs and trees there is storage of organic matter in the lower part of the trunk and in the roots, and that, as growth starts in the spring, this food becomes soluble and passes upward through the xylem to the developing shoots and leaves.

The fact that has been most commonly offered as proof of upward translocation through the xylem is that the xylem tissues of woody plants commonly contain quantities of organic storage products, particularly sugars and starches. It has been shown by Atkins (1916), Fischer (1891), and others that not only the living parenchyma cells but also the water-conducting cells proper, the tracheae and tracheids, contain appreciable quantities of soluble carbohydrates, and Atkins has found these to be present at all seasons of the year. The latter considers that sugars are commonly carried through the xylem. He even goes so far as to say that ". . . the transference of carbohydrates can no longer be regarded as an occasional and accessory function of the vessels, but is certainly a continual and principal function . . . ." It may well be, however, that there is no flow of solution through the xylem for any great distance, for a possible frequent interposition of living cells across the water-conducting tissues may prevent such a flow. Atkins himself clearly recognizes that water may flow across tissues containing a high solute content without carrying the solutes with it.

Experiments performed by Hartig (1858) are also commonly cited in texts as offering proof of upward translocation through the xylem. Hartig ringed a number of trees early in the summer and found early in the following spring that the starch stored below the ring had disappeared. He concluded that the storage products must have been translocated upward through the xylem. It might be, however, that the food stored below the ring was used locally for growth in diameter, or that it was translocated downward through the phloem and was used in root growth.

In order to determine more definitely whether the upward translocation of food takes place primarily through the phloem or through the xylem, the writer has conducted a series of experiments part of which are reported in this paper. Some of these experiments also throw light on the matter of food movement from roots or trunks to growing shoots. The discussion therefore naturally falls into two main parts: (1) When upward translocation of organic matter takes place, as it certainly must for at least short distances, does it take place through the water-conducting tissues, the xylem, or

through the phloem? And (2) Is there normally an upward movement of this food from the roots and lower trunk to the growing shoot? The present discussion will deal with the former question; the second question will be discussed in a subsequent paper.

EFFECT OF RINGING ON GROWTH OF LEAFY AND DEFOLIATED SHOOTS.

Vigorous young shoots of *Philadelphus pubescens* Loisel. were treated on May 30 as indicated in table 1. In this as in subsequent tables those shoots having the same letter were fairly well matched as to size, vigor, and position on parent plant.

TABLE 1. *Philadelphus pubescens. Rings in new growth 15–20 cm. from tip. Stems measured from attachment to main stem. May 30 to June 8, 1918*

	1 Not Ringed. Leaves Remaining			2 Ringed 15–20 Cm. from Tip. Leaves Remaining			3 Not Ringed. Leaves Removed from Upper 15–20 Cm.			4 Ringed 15–20 Cm. from Tip. Leaves Above Ring Removed		
	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 8	Gain in Cm.
a	52.5	81.5	28.5	61.0	79.0	18.0	40.0	69.0	29.0	58.5	58.5	0.0
b....	58.0	79.5	21.5	60.0	75.0	15.0	53.5	85.0	31.5	60.5	61.5	1.0
c....	49.5	85.0	35.5	78.0	Broken	—	40.5	66.0	25.5	63.5	81.5	18.0[1]
d....	54.0	90.0	45.0	61.0	67.0	6.0	64.0	92.5	28.5	55.0	55.5	0.5
e	59.0	99.0	40.0	59.0	67.0	8.0	60.0	80.5	20.5	58.0	80.0	22.0[1]
Average gain			34.1			11.75			27.0			0.5

The measurements of June 8 show very clearly that ringing has in some way checked the growth of the shoots. The simplest explanation appears to be that the food necessary for shoot formation passes upward through the phloem and not through the xylem tissues. The few leaves present above the ring (group 2) are able to synthesize sufficient food to allow for some growth. In two shoots of group 4 a narrow strip of phloem was left by accident, and this has served to transfer sufficient food to allow for considerable growth. Two or three small leaves unfolded at the apex of the stems of group 4, but these were too small to carry on much photosynthesis, so growth continued very slowly for several weeks until other leaves had developed.

The same experiment was repeated with Philadelphus in the spring of 1919, except that in this case, instead of making the ring in the upper part of the new growth, the ringing was done on the wood of the previous year just below the bases of the young shoots. As the stems had been cut back when dormant, this left the new shoots at the apex of the stem. In each case, whether the leaves were or were not removed, one pair of leaves enclosing the growing tip was removed. The measurements are recorded in table 2, and a photograph of those shoots lettered *g* is shown in figure 1.

[1] Not included in average. A strip of phloem was left on about ¼ of the circumference. The twig was bent at an angle at this point.

TABLE 2. *Philadelphus pubescens. Paired shoots measured from attachment to old stem. Rings made on old wood just below attachment of young shoots. May and June, 1919*

	1 Not Ringed. Leaves Remaining			2 Ringed. Leaves Remaining			3 Not Ringed. Leaves Removed			4 Ringed. Leaves Removed		
	Length in Cm. May 30	Length in Cm. June 4	Gain in Cm.	Length in Cm. May 30	Length in Cm. June 4	Gain in Cm.	Length in Mm. May 30	Length in Mm. June 4	Gain in Mm.	Length in Mm. May 30	Length in Mm. June 4	Gain in Mm.
a	19.0	35.5	17.5	16.0	27.5	11.5	4.0	10.5	6.5	14.0	15.5	1.5
	18.5	33.5	15.0	14.5	26.5	12.0	16.0	27.5	11.5	12.5	14.0	1.5
b	17.0	30.5	13.5	15.0	27.5	12.5	13.0	20.5	7.5	19.0	21.5	2.5
	17.5	31.5	14.0	18.5	31.5	13.0	14.5	22.5	8.0	16.5	17.5	1.0
	25.5	46.5	21.0	21.0	29.0	8.0	19.5	26.0	7.5	15.0	16.0	1.0
c	13.0	30.0	17.0	23.0	35.0	12.0	18.0	22.5	4.5	19.0	20.5	1.5
	23.0	40.5	17.5	20.5	35.0	14.5	17.0	25.0	8.0	16.5	15.5	2.0
d	23.0	42.0	19.0	24.0	38.0	14.0	15.0	24.0	9.0	20.0	21.5	1.5
	12.5	28.0	15.5	24.0	39.5	15.5	16.0	25.0	9.0	15.5	17.0	1.5
e	18.5	35.0	16.5	24.5	40.0	15.5	23.0	35.5	12.5	15.5	17.0	1.5
	20.0	36.5	16.5	21.5	33.5	12.0	16.5	19.0	2.5	20.0	22.5	2.5
f	20.0	38.5	18.5	21.5	35.0	13.5	24.5	28.0	3.5	20.5	22.5	2.0
	15.5	29.0	13.5	24.5	38.0	13.5	24.5	30.0	5.5	28.5	30.0	1.5
g	20.5	34.5	14.0	27.5	41.5	14.0	21.5	27.5	6.0	26.5	27.5	1.0
Ave.			16.36			12.96			7.96			1.61

	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.	Length in Mm. June 3	Length in Mm. June 6	Gain in Mm.
h	32.0	39.5	7.5	38.0	45.0	7.0	45.0	47.5	2.5	24.0	25.5	1.5
	27.0	35.0	8.0	33.0	40.0	7.0	43.0	46.5	3.5	38.0	38.5	0.
	28.0	36.0	8.0	41.5	49.0	7.5	36.5	40.0	3.5	36.0	37.5	1-
i	43.0	53.5	10.5	38.0	45.5	7.5	26.5	29.5	3.0	25.5	27.5	(1
	42.5	54.0	11.5	42.5	51.0	8.5	44.5	48.0	3.5	35.0	36.5	
k	42.5	52.5	10.0	31.5	38.5	7.0	37.0	40.0	3.0	30.5	32.0	
	42.5	52.5	10.0	40.5	47.0	6.5	46.0	50.5	4.0	28.5	30.0	
l	43.5	53.0	9.5	42.0	48.0	6.0	41.5	46.5	5.0	28.5	30.0	
Ave.			9.38			7.13			3.56			

The results of this second experiment are similar to those of the previous one. It is noticeable, however, that the ringed shoots with leaves (group 2) in this experiment show greater growth than shoots without leaves and not ringed (group 3), while in the previous experiment the reverse was true. In the experiment of 1918 only a third to a half of the new shoot was above the ring or was leafless, while in that of 1919 the whole of each new shoot was above the ring. It seems very probable that the older leaves of the new shoot manufacture a large part of the food used in terminal growth after the shoot is well started.

A similar experiment was tried with a tree of Northern Spy apple. This was started near the end of the growing season, which fact accounts for the small amount of growth obtained. All growth on this tree was practically completed by June 30, whereas with most of the other trees of the orchard it was nearly completed on June 11.[2]

TABLE 3. *Pyrus malus (Northern Spy). Rings made 15 cm. from tip in present year's growth. Measurements from last bud scale scar to tip. June 11 to June 30, 1918. All growth was practically completed by June 30*

	1 Not Ringed. Leaves Remaining			2 Ringed. Leaves Remaining			3 Not Ringed. Leaves Removed			4 Ringed. Leaves Removed		
	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.	Length in Cm. June 11	Length in Cm. June 30	Gain in Cm.
a....	26.2	30.5	4.3	24.5	30.0	5.5	23.0	25.5	2.5	23.3	23.0	0.0
b....	26.0	29.5	3.5	17.5	22.0	4.5	24.8	28.0	3.2	21.5	21.0	0.0
c....	26.5	32.5	6.0	23.5	Broken	—	19.5	23.5	4.5	24.5	25.0	0.5
d....	25.0	29.5	4.5	20.0	24.5	4.5	23.3	28.0	4.7	22.5	23.0	0.5
e....	20.7	22.0	1.3	26.5	32.5	6.0	24.0	24.5	0.5	22.4	24.5	0.1
f....	25.7	33.0	7.3	23.0	29.0	6.0	22.2	27.0	4.8	24.6	25.0	0.4
Ave.			4.48			5.3			3.37			0.25

It is to be noted in this case that the ringed twigs which retained their leaves made a growth greater than did similar twigs not ringed. This difference is not striking, but in only one pair (*f*) is there greater growth of the stem not ringed. It would seem that food manufactured by the leaves was beginning to be removed downward and that the ring had checked this removal, thus increasing the supply for continued apical growth. The *d*. al cessation of growth of all twigs is evidently brought about by conditions *e*·· elated with the rest period which will not be discussed here. The Avera|t complete lack of growth of the ringed twigs that had been deprived r leaves coincides with the similar results obtained with Philadelphus.

Th.tly ringing has entirely prevented the upward translocation of some way ch.l or materials necessary for growth.

to be ther experiments of the same nature were tried with *Ligustrum* the pl*ium* Hassk. Sone of the results obtained are presented in table 4. above experiments showed results practically identical with these, so it is some necessary to present all of them.

by arom these experiments it seems very clear that the ringing has presid.ted the upward movement of some substance or substances necessary st. growth. When leaves are present above a ring, these produce enough of s.is substance to allow for continued growth. Evidently the check in growth is not due to lack of water resulting from injury to the xylem, for those stems that were ringed but retained their leaves always made fair growth, which occasionally even exceeded that of the checks. Under certain conditions, however, ringing does seem to be followed by withering of the parts above the ring. This occurs especially when the ring is fairly near the young tip but only when no leaves are left above the ring. Hanstein (1860) obtained similar results and concluded that lack of water cannot be the cause of the withering, for when leaves remain above the ring, certainly more water is necessary but growth continues, while the shorter the part above the ring the less water it will need but the quicker is its death, even in a moist atmosphere.

TABLE 4. *Ligustrum ovalifolium. Bushes killed nearly to the ground by the cold winter. Experiments with the strong young shoots, June, 1918. All ring wounds had healed over by August 1. Some of no. 4, however, were not perfectly healed*

Hedge No. 1	1 Not Ringed. Leaves Remaining		2 Ringed 20-24 Cm. from Top. Leaves Remaining		3 Not Ringed. Leaves Removed for a Distance of 20-24 Cm. from Top		4 Ringed 20-24 Cm. from Top. Leaves Above Ring Removed	
	Growth in Cm. June 18-July 3	Growth in Cm. July 3-Aug. 1	Growth in Cm. June 18-July 3	Growth in Cm. July 3-Aug. 1	Growth in Cm. June 18-July 3	Growth in Cm. July 3-Aug. 1	Growth in Cm. June 18-July 3	Growth in Cm. July 3-Aug. 1
a........	15.0	33.5	15.0	23.5	7.5	26.5	0.5	14.5
b........	15.0	32.5	16.0	29.5	9.5	34.5	1.0	12.0
c........	13.8	31.5	12.3	20.5	8.0	28.0	1.0	10.0
d........	10.5	27.5	14.5	27.5	7.5	21.0	1.0	15.5
e........	9.0	20.0	15.0	20.0	5.5	16.0	0.5	12.0
f........	15.0	25.0	15.5	broken	6.5	10.5	0.5	9.5
g........	17.0	32.5	14.0	27.0			0.5	13.0
Ave.....	13.61	28.93	14.61	24.67	7.41	22.75	0.71	12.36
Hedge No. 2	Growth in Cm. June 19-July 3	Growth in Cm. July 3-Aug. 1	Growth in Cm. June 19-July 3	Growth in Cm. July 3-Aug. 1	Growth in Cm. June 19-July 3	Growth in Cm. July 3-Aug. 1	Growth in Cm. June 19-July 3	Growth in Cm. July 3-Aug. 1
h........	15.0	30.0	15.0	13.0	3.5	25.0	0.4	16.1
i........	11.0	18.5	10.0	11.5	5.5	19.5	0.5	1.0
j........	13.5	17.0	11.5	12.0	8.0	15.0	0.0	13.0
k........	12.5	26.0	9.0	broken	7.0	12.0	0.0	5.5
l........	10.0	29.5	9.5	9.0	6.5	18.0	0.0	2.2
m........	12.5	22.5	8.5	3.0	4.0	broken	0.5	5.0
Ave.....	12.49	22.41	10.58	9.7	5.75	17.9	0.23	7.11

Hanstein explained this lack of growth and the death above a ring when the leaves are removed on the grounds that "newly assimilated sap" is necessary. He accepted Hartig's idea that the stored food, particularly carbohydrates, readily moves upward through the xylem, but believed that this newly assimilated food moves in the phloem only. When leaves remain above a ring, they supply this essential food. Furthermore, Hanstein found that ringed willow cuttings placed in dry air showed a withering of the phloem above the ring while the presence of leaves prevented withering. He concluded that water cannot readily move from xylem to phloem and that the leaves aid in this transfer. According to his ideas, therefore, the leaves supply "newly assimilated sap "which is necessary for growth and can be carried through the phloem only, and they aid in transmitting the water to the phloem when the latter is separated from the roots by a ring.

If, however, all foods, including sugars, were translocated upward through the phloem only and not through the xylem, ringing would check further growth by withholding all necessary foods, and the withering might be due therefore not to the lack of any particular food, newly assimilated or otherwise, but to a deficiency of osmotically active substances, perhaps carbohydrates. Chandler (1914) has clearly demonstrated that, if tissues having different osmotic concentrations are organically connected, that

tissue having the higher concentration will withdraw water from the other, causing the latter to wither.   He demonstrated that leaves may withdraw water from fruits, or that a tomato plant having a high sugar content, if grafted to one with a lower sugar content, may withdraw water from the latter, causing it to wither.

In order to determine whether ringing and defoliation have any effect on the concentration of the sap, the freezing points of the sap from some of the stems of Philadelphus, previously described in table 2, were determined. The shoots were in pairs, as shown in figure 1, and for each determination both stems of the pair were used.   As soon as possible after cutting the shoots, the leaves were removed and the stems were immediately cut into

FIG. 1. . Effects of ringing on leafy and defoliated shoots of Philadelphus.
1. Not ringed, leaves remaining.
2. Ringed, leaves remaining.
3. Not ringed, leaves removed.
4. Ringed, leaves removed.
Black strings tied at *x* indicate the original length of the shoots.

short pieces and placed in large test tubes which were then quickly plunged into a freezing mixture.   After the tissues were thoroughly frozen they were ground in a mortar and the freezing point of the pulpy mass was determined. The material from each of numbers 1, 3, and 4 was extracted in 80 percent alcohol and this extract was hydrolyzed and analyzed for reducing sugars. The total sugar found, expressed as invert sugar, is recorded with the other

data in table 5. In table 6 are given the freezing point lowerings of the terminal pair as well as of the first pair of stems below the terminal pair. These were determined for the same series but on a different day.

TABLE 5. *Philadelphus pubescens. Effect of ringing and removal of leaves on growth osmotic concentration, and soluble sugar content of the stem*

		Length of Shoots in Cm. May 30	Length of Shoots in Cm. June 4	Gain in Cm. Length	Ave. Gain per Pair.	Freezing Point Depression Δ	Green Weight	Total Dry Weight	Mg. Invert Sugar per Gm. Green Weight	Mg. Invert Sugar per Gm. Dry Weight
1. Not ringed, leaves present.........	a	19.0	36.5	17.5			10.0			
		18.5	33.5	15.0	16.25	0.65°				
	d	23.0	40.5	17.5						
		23.0	42.0	19.0	18.75	0.69°	15.6	1.74	7.81	114.9
2. Ringed, leaves present..............	a	16.0	27.5	11.5						
		14.5	26.5	12.0	11.75	0.60⁵	8.9			
	d	20.5	35.0	14.5						
		24.0	38.0	14.0	14.25	0.62°	12.0	—	—	—
3. Not ringed, leaves removed.........	a	4.0	10.5	6.5						
		16.0	27.5	11.5	9.00	0.61°	4.7			
	d	17.0	25.0	8.0						
		15.0	24.0	9.0	8.50	0.61°	4.9	0.64	4.5	67.6
4. Ringed, leaves removed.........	a	14.0	15.5	1.5						
		12.5	14.0	1.5	1.50	0.455°	2.7			
	d	16.5	18.5	2.0						
		20.0	21.5	1.5	1.75	0.52°	6.4	0.445	2.6	52.2

TABLE 6. *Philadelphus pubescens. Effect of ringing and removal of leaves on osmotic concentration of the stem as compared with the concentration of lower shoots of the same stem*

		Total Gain for Each Pair of Shoots, May 30–June 4	Green Weights	Δ	Green Weight of First Shoots Below	Δ of First Shoots Below
1. Not ringed, leaves present	(e).......	320	9.5	0.61	10.2	0.615
	(f).......	350	12.9[a]	0.62	4.4	0.62
2. Ringed, leaves present	(e).......	310	16.8	0.63	8.2[a]	0.675
	(f).......	255	8.8	0.63	12.9	—
3. Not ringed, leaves removed	(e).......	215	10.0	0.585	10.1[a]	0.59
	(f).......	60	5.3	0.61	6.8[a]	0.57
4. Ringed, leaves removed	(e).......	30	4.8	0.53	5.3	0.655
	(f).......	45	6.3	0.59	—	0.66

The cryoscopic data thus far obtained are not sufficiently extensive to warrant a detailed discussion, but they clearly show that the ringing of a defoliated shoot results in a distinct falling off of the osmotic concentration of that shoot. Whether the check in growth is due primarily to a lack of food necessary for energy or for building material, or to lack of water result-

[a] These are single shoots, not pairs.

ing from a deficiency of osmotically active substances, is not clear. From
the available data it would seem, however, that the former is of first im-
portance. In a number of instances it was found that the part above a ring
would grow slightly, and later would wither completely when the compe-
tition for water became more severe. Table 6 indicates, that, as would be
expected, the ringing not only decreases the concentration above the ring
but also tends to increase that below.

These few determinations cannot be fully relied upon for all details, but,
assuming that they are approximately correct, it can be readily seen why the
part above a ring cannot compete for water with other parts unless it retains
its leaves. This therefore would explain the withering of ringed shoots
that lack leaves, and shows that the leaves do not directly draw water to
the phloem as suggested by Hanstein, but rather that they supply the
phloem with osmotically active substances, thus indirectly enabling it to
obtain its own water.

It might be stated in this connection that the writer has obtained con-
siderable evidence that one important factor among several possible factors
that may be concerned in the matter of polarity and inhibition is associated
with a local distribution of foods and of osmotically active substances.
The same substance, possibly sugar, may act in both rôles. It has been
found, for instance, that the upper part of a rapidly growing shoot may have
a concentration that would give a pressure over two atmospheres greater
than the concentration in the middle or lower part of the same shoot.
The "inhibition" of shoot growth at nodes below the terminal one may be
due to a lack of sufficient food and to inability to compete successfully for
water rather than to a backward flow of some "inhibitor." In fact, as was
shown in a previous paper (Curtis, 1918), it is possible to reverse the
polarity by placing the base of a shoot in a strong sucrose solution. The
writer has found that other substances are even more efficient than sucrose
in thus altering the polarity of a shoot. The check in growth following
ringing cannot be due to retardation in removal of an "inhibitor" produced
by the leaves, for, if leaves remain, the growth is greater than if they are
removed.

The Translocation of Food to Fruits

It has been recognized that at least part of the food carried to growing
fruits probably moves through the phloem. Hanstein (1860) found that
ringing below fruits, if no leaves were left above the ring, resulted in checking
their further development. In order to determine the effect of ringing on
the transfer of food to fruits, twelve fairly well matched pairs of young
Wealthy apples were selected. The leaves from the stems close to the fruit
were removed, and the stem of one of each pair was ringed so that no leaves
were above the ring. The greatest length and the greatest diameter of each
fruit were taken. The same thing was done with three pairs of Rhode

TABLE 7. *Pyrus malus.* Effect of ringing on movement of food to fruit. Leaves removed above ring and lo ... ringed except in No. 3 (o) in which case leaves were left above ring

		Aug. 6, 1918		Sept. 25, 1918						Relative Gain in Approximate Volume. Check as Unity	Relative Green Weight. Check as Unity	Relative Dry Weight. Check as Unity
		Average of Length and Diameter, Mm.	Approximate Volume, Cc.	Average of Length and Diameter, Mm.	Approximate Volume, Cc.	Gain in Approximate Volume, Cc.	Green Weight, Gm.	Dry Weight, Gm.				
1. Wealthy not ringed	c	45	47.66	63	130.77	83.11	113.8	16.74			
	d	43	41.58	45.5	49.26	7.68	63.0	7.82			
	e	40.5	34.74	52.0	83.54	48.80	71.2	10.30			
	f	45.5	49.26	57	96.86	47.60	88.6	11.80			
	i	41	36.05	56.5	94.33	58.28	85.9	11.74			
	j	44	44.55	54.5	84.66	40.11	72.1	10.00			
	Ave.	43.17	42.31	54.75	89.90	47.60	82.43	11.40		1.00	1.00
Wealthy ringed	b	41.5	37.38	42.5	40.15	2.77	36.9	4.80			
	d	46.5	52.58	46	50.91	-1.68	47.8	6.66			
	f	41.5	37.38	42	38.75	1.37	38.0	5.05			
	g	41.5	37.38	40.5	34.74	-2.64	33.6	4.98			
	h	37.75	28.14	38.5	29.90	1.76	27.7	3.70			
	i	40.75	35.39	41.5	37.38	1.99	38.0	5.03			
	k	45.5	49.26	46.5	52.58	3.32	47.1	5.48			
	l	41.5	37.38	42	38.75	1.37	39.5	5.06			
	Ave.	42.06	39.36	42.44	40.40	1.03	38.58	5.10	0.02	0.47	0.45
2. Rhode Island Greening not ringed	m	48.5	59.67	63	130.77	71.10	121.7	18.43			
	n	48.0	57.84	55.5	89.41	34.57	93.4	13.90			
	o	52.0	83.54	67	157.30	73.76	154.7	21.53			
	Ave.	49.5	67.02	61.8	125.83	58.81	123.3	17.95		1.00	1.00
Rhode Island Greening ringed	m	48	57.84	49.5	63.43	5.59	60.5	8.80			
	n	48	57.84	49	61.53	3.69	62.7	8.86			
	o	51	69.38	53	77.86	8.48	77.3	9.48			
	Ave.	49.0	61.69	59.5	67.61	5.92	66.83	9.05	0.10	0.54	0.50
3. Rhode Island Greening ringed with leaves	o	52.5	75.68	57	96.86	21.18	92.40	12.61	0.36	0.75	0.71

Island Greenings, and in addition two stems were left without removing
the leaves above the ring. The fruit was gathered on September 25 at
which time a number had fallen from the trees, which fact accounts for the
missing apples. The average of the greatest length and the greatest
diameter was taken as the diameter of a sphere and the volume of this
sphere was calculated. The data are presented in table 7.

There seems to have been practically no increase in the volume of the
apples on the ringed stems. The 2 percent recorded is possibly within the
range of probable error. Whether there was a transfer of anything but
water to the fruits cannot be definitely determined from the data available,
but the fact that both the water content of the fruit from the ringed stem
and the volume-dry weight ratio of the same fruit were greater than in the
fruit from the stem that was not ringed, as well as greater than in samples
taken at the time of ringing, would indicate that no appreciable amount of
food had moved to the fruit. The water contents of the fruit from the
ringed stem, of that from the unringed stem, and of that taken at the time
of ringing were respectively 86.9 percent, 86.2 percent, and 85.0 percent,
and the approximate volume-dry weight ratios were respectively 7.92,
7.89, and 7.05.

EFFECT OF RINGING DORMANT TWIGS IN THE SPRING

Dormant stems of various woody plants were ringed at different distances
from the tip to determine whether food stored in the xylem would move
longitudinally through the same tissues and to determine from how far

FIG. 2. Crataegus ringed, while dormant, at different distances from the tip. The
place of ringing is indicated by R. In the stem marked R* a narrow strip of phloem less
than one fourth the circumference was left. Similar results were obtained when only one
half of the xylem and one fourth of the phloem were left. (The unringed twig of the group
at the right was omitted by the engraver. This twig showed a growth almost identical to
that of R.*)

ck the food supply was drawn. In all cases starch was present in the
lem at the time of ringing. Results obtained when twigs of Crataegus
re ringed in this way are shown in table 8.

TABLE 8. *Crataegus sp. Ringed April 8. Measured May 8*

X. Check not ringed.

Ringed in 2nd internode from tip.

Ringed in 4th internode from tip.

Ringed at base of one-year-old wood, usually the 7th or 8th internode.

Ringed back on three- or four-year-old wood.

Those marked z had half the xylem cut away and three fourths of the phloem. One fourth of the phloem was left.

Lateral buds removed from all.

	X	A	Az	B	Bz	C	D
1................	20	0	—	0	—	16	16
2................	25	14	20	broken	—	16	20
3................	25	2	—	—	—	—	17
4................	25	3	—	8	—	9	—
5................	28	4	—	4	20	—	15
6................	25	6	27	4	—	—	20
7................	35	8	32	8	—	25	30
8................	30	3	—	broken	—	—	—
9................	20	—	—	6	30	20	—
10................	28	6	28	5	—	22	21
11................	27	broken	—	broken	—	—	—
12................	25	—	20	9	—	—	30
13................	30	6	9[4]	10	32	—	—
14................	25	9	10[4]	13	30	—	28
15................	28	7	9[4]	13	—	18	—
16................	30	12	8[4]	16	—	—	25
17................	30	—	30	9	—	10	20
Ave.............	26.8	6.1	26.2	8.1	28.0	17.0	22.0

From these results it is apparent that material carried by the phloem is necessary for shoot growth. The check in growth cannot be due to any injury to the xylem, for if half the xylem is cut away and but a quarter of the phloem is left, growth is practically normal. This is shown in the columns Az and Bz of table 8 and in figure 2. Two possible explanations occur. Either the xylem carries no foods, neither carbohydrates nor nitrogenous material, or the xylem carries certain foods, perhaps carbohydrates, while the phloem carries some other substances, possibly nitrogenous, which may be necessary for growth. If the second alternative were true, the greater the amount of phloem above the ring the greater would be the supply of this substance which may act as a limiting factor. The following data, however (table 9), offer strong evidence that the carbohydrate supply is the limiting factor and that this cannot move upward through the xylem.

[4] These results are not included in the averages, for the wounds were not paraffined and the xylem had dried out checking the growth of the shoot.

TABLE 9. *Crataegus sp. April to May 18, 1919*

X. Check, not ringed.
A. Ringed at the second internode below the terminal bud.
B. Ringed at the fourth internode below the terminal bud.
C. Ringed at the seventh or eighth internode below the terminal bud.
    All lateral buds were removed in each case.

No.	X		A		B		C	
	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves
1.......	65	5	0		0	dried	8	3
2.......	70	7	7	(green only	15	2	35	4
3.......	85	8	0		15	3	30	—
4.......	45	4	(a) 1 (b) 0	(green only)	10^5	1	35	3
5.......	40	5	0	dried	20	(green only)	35	4
6.......	35	8	6	(green only)	15	(green only)	10	green
7.......	70	—	(a) 6 (b) 30^5	(green only)	12	(green only)	20	—
8.......	(a) 55 (b) 50	5 5	0 60^5	dried 5	0	dead	30	2
Ave.....	57.2	6.2	2.2	0	11.0	0.5	25.4	2.7

Starch tests:

X. Starch fairly abundant in primary xylem, pith, medullary rays, and outer cortex both near the tip and near the base. In nos. 2, 3, 4, 7, 8a, and 8b, cambial growth was started and starch had largely disappeared from the outer part of the medullary rays.

A. No trace of starch above rings except in no. 5 which contained traces in the pith. Below rings just as in checks. Nos. 4, 6, and 7 tested for starch in region of ring showed none in upper part, traces in middle, similar to check in lower part.

B. No traces of starch above rings, except in nos. 1 and 8 which had evidently died early. Below rings just as in checks. Nos. 5, 6, and 7 tested for starch in region of ring showed none in upper part, while the lower part appeared about the same as just below the ring.[6]

C. No starch above the rings, except in no. 6 in which the terminal bud had been broken off and adventitious buds were just starting. In three cases there were slight traces in 2–3 pith cells. Below rings starch was fairly abundant as in the check stems.

In each case in which growth had ceased, the starch above the ring had disappeared. If something other than sugar were the limiting factor, one would expect that the starch could not be utilized, yet the shorter the piece above the ring the more rapid was the disappearance of the starch and the earlier the cessation of growth. In a few exceptions with Crataegus and Acer a very short piece above a ring sometimes died before all the starch

[5] In these twigs a narrow strip of phloem was left covering less than one fourth of the circumference.

[6] In no. 4 a narrow strip of phloem had healed over under the paraffin. Starch was fairly abundant in primary xylem, pith, and medullary rays. None in cortex. Below ring same as in checks.

,d disappeared. In the checks, on the other hand, the starch had not ¡ disappeared at the time the data of table 9 were taken. Later, however, the shoot growth neared completion, starch disappeared from the checks .so. It is evident that, when the stem is not ringed, a shoot does not ,st deplete the starch in its immediate neighborhood, but the starch for ,me distance is reduced rather uniformly.

TABLE 10. *Acer saccharum. Ringed April 7, 1919.*
Ringed in middle of first year's growth

	Growth in Mm. by May 11		Notes
	Ringed Branch	Corresponding Branch Not Ringed	
1 ...	10	55	*May 11*, nos. 1, 4, and 5 and their corresponding check twigs were cut and tested for starch.
2 ...	20	35	*Above ring:* In each case no trace of starch present above the ring; neither directly under the terminal node, in the middle internode, nor in the basal internode.
3 ...	10	80	
4 ...	15	90	
5 ...	12	90	
6 ...	15	55	*Below ring:* Starch present in each case in the primary xylem and in the medullary rays in all parts below the rings.
Ave.	13.7	67.5	*Within the ring:* Starch present as below the ring. *Check:* Starch present in each stem in the primary xylem and in the medullary rays in all parts corresponding to those tested in the ringed stems. *May 16*, all starch had disappeared from check stems as well as from the ringed ones.

Ringed at base of first year's growth.

	Growth in Mm. by May 11		Growth in Mm. by May 24		Notes
	Ringed Branch	Corresponding Branch Not Ringed	Ringed Branch	Corresponding Branch Not Ringed	
1 ...	45	80	65	205	*May 11*, no. 4 and its corresponding check were cut and tested for starch.
2 ...	45	80	75	180	*Above ring:* No trace of starch in any part.
3 ...	50	80	85	210	
4 ...	45	90	—	—	*Below ring:* Starch present in primary xylem and in medullary rays.
5 ...	35	55	80	240	
Ave.	44.0	77.0	76.3	208.8	*Within ring:* Starch in primary xylem and in medullary rays. *Check:* Starch in primary xylem and in medullary rays in all regions corresponding to those tested in the ringed stems.

The sugar maple is commonly cited as an example of a tree that transfers its carbohydrates upward through the xylem. The trees were bleeding freely at the time the ringing was done, yet practically no translocation of carbohydrates occurred longitudinally through the xylem.

Very similar results were obtained with the pear, *Pyrus communis*, and the beech, *Fagus grandifolia.* In both, the nearer the ring was to the tip, the less was the growth and the sooner did the starch disappear above the ring. The measurements for the beech are given in table 11 and a photograph of series no. 2 in figure 3.

TABLE II. *Fagus grandifolia. April 7 to May 24*

X. Check twigs not ringed.
B. Ringed in the middle of the one-year-old wood.
C. Ringed at the base of the one-year-old wood.
D. Ringed in the wood three to five years old which in all cases was under one centimeter diameter.

All having the same number were fairly well matched at the time of ringing.

	X		B		C		D	
	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves.	Length in Mm.	Number of Leaves	Length in Mm.	Number of Leaves
1........	100	5	10	4	20	5	30	5
2........	130	5	35	4	50	5	30	4
3........	365	9	50	5	110	7	—	—
4........	170	6	10	0	17	0	60	6
5........	240	8	15	0	—	—	100	6
6........	155	7	15	0	30	0	20	4
7........	145	6	15	2	30	3	115	5
Ave....	186.4	6.6	21.4	2.1	42.8	3.3	59.1	5.0

One of Hartig's chief arguments that carbohydrates move upward through the xylem was based on the fact that, if a tree was ringed, the starch
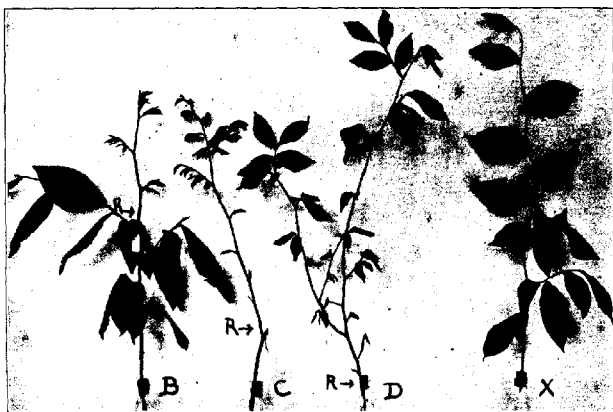

FIG. 3. *Fagus grandiflora* ringed, while dormant, at different distances from the tip. The point of ringing is indicated by *R*.

below the ring disappeared. He assumed that it moved upward, but there is no reason why it could not have been moved radially and used in cambial growth, or moved downward through the phloem to the growing roots. To test this latter possibility, experiments were tried with *Ostrya virginiana*

.ch, *Crataegus* sp., *Acer saccharum* Marsh., and *Fagus grandifolia* Ehrh., which two rings were made on the same stem some distance apart.

Stems of Ostrya were ringed April 6. By May 6 growth had started and he shoots of the ringed and unringed stems were apparently of the same ength, measuring for the most part about 15 to 20 millimeters. The shoots f the ringed stem, however, had used up most of their reserve food, for
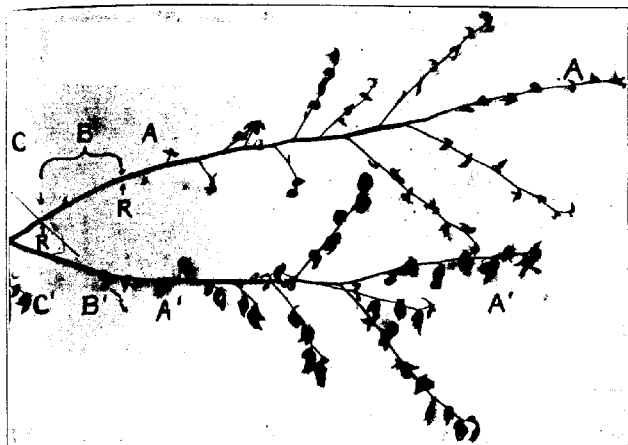

Fig. 4. *Ostrya virginiana* ringed April 6 at *RR*. Cut May 19 and tested for starch with Iodine.

Ringed.   *A*. Above upper ring. No trace of starch in any part either in the young twigs or in the older stem.

B. Between rings. Starch very abundant in pith, medullary rays, cortex and phloem parenchyma.

C. Below lower ring. Traces of starch in the pith cells. (See page 116 for results as to upper, middle, and lower parts of upper ring.)

Not ringed.   *A* . Traces of starch in pith cells.

B . Traces of starch in pith cells.

C . Traces of starch in pith cells.

very little further growth took place while the shoots of the check stem continued to grow. On May 19 two of these stems were cut and tested for starch. For the stem shown in the photograph (fig. 4) the tests were as follows:

Above the upper ring: No trace of starch was present in any part, either in the young twigs or in the older stem.

Between the two rings: Starch was very abundant in the pith, medullary rays, and cortex.

Below the lower ring: There were traces of starch in the pith.

Upper part of upper ring: There was no trace of starch.

Middle part of upper ring: There were traces of starch in the pith an l in some of the medullary ray cells.

Lower part of upper ring: Starch was abundant in pith and medullar , rays, similar to that between rings.

Check: There were traces of starch in the pith cells in the regions corresponding to those listed above.

In the other stem tested at the same time the results were practically the same. There was more starch in the check, however, which showed very distinct traces in the pith and very slight traces in the medullary rays and cortex. In both stems the results were striking. When the sections stained with iodine were held against white paper and observed from across the room, the sections from between rings appeared almost black and the others practically colorless. These results indicate that there is practically no longitudinal transfer of carbohydrates through the xylem.

A similar experiment in double ringing was performed with several species of Crataegus. Stems were ringed April 6 and examined May 17. All showed results similar to those obtained with Ostrya; that is, in all cases starch had disappeared above the upper ring, was abundant between the rings, and was present in moderate amounts below the lower ring and in the check stems. Between the rings, starch was very abundant in the primary xylem and medullary rays; but the results were not as striking as those obtained with Ostrya, for the stem at no time contained as much starch in the pith and therefore did not appear as dark when stained with iodine.

A number of stems of *Acer saccharum* ranging in diameter from 4.5 mm. to 24.3 mm. were double-ringed on April 6 and 7. The distances between the rings ranged from 15 cm. to 107 cm. At the time of ringing most of the stems were bleeding freely. A number of the stems were cut between May 6 and May 19. In all cases starch was completely or almost completely absent above the upper ring, very abundant between rings and nearly absent to fairly abundant below the lower ring, depending on the time of cutting and the position on the tree. The data obtained from one such stem are recorded below and in table 12. This branch showed 15 annual rings at the lower ring; it was 24.5 mm. in diameter at this point, which was situated 16 cm. from the main trunk. At the level of the second ring, which was 107 cm. from the first, the diameter of the branch was 20.2 mm. The check branch was not perfectly matched but was somewhat smaller than the ringed one. The diameter at its base was 22.3 mm.

Above the upper ring: There was no starch in any part except in a few scattering cells of the primary xylem.

Between the two rings: Starch was very abundant in the primary xylem and the medullary rays.

Below the lower ring: Starch was fairly abundant in the primary xylem ⁝ in the inner part of the medullary rays. The medullary rays of the ⁝ r annual ring were emptied of starch, those of the second contained ⁝ traces, those of the third still larger amounts, while in the fourth annual ⁝ the starch was abundant.

Check: At the base starch was fairly abundant in the primary xylem a⁝ in the medullary rays of the inner annual rings, disappearing in the th⁝rd ring and entirely absent in the outer two. Farther out on the stem, a⁝ a point corresponding to that of the upper ring on the ringed branch, the diameter was 20.5 mm. At this point starch was mostly absent from the outer nine rings but was fairly abundant in the inner four. Still farther out, where the diameter was 12 mm., starch was present in distinct quantities in the primary xylem only.

The stems were cut in pieces 12 cm. long, which were then peeled to the cambium. These pieces of xylem were centrifuged and the small amount of sap obtained was hydrolyzed with hydrochloric acid and tested for reducing sugar. Samples corresponding to 1 cc. amounts from the stems immediately above the upper ring and between the rings were tested. From above the ring 0.3 mg. of cuprous oxide was obtained on boiling with Fehling's solution, while 2.0 mg. were obtained from between the rings. A second test was lost by accident, but at the time of filtering through the asbestos there was a very distinct precipitate of the cuprous oxide from the sample between the rings and but a very faint trace of the oxide from the other sample. Another accident resulted in the loss of the remainder of the sap, so no further tests could be made.

Samples of the oven-dried wood were sawed into 5 mm. lengths and extracted in 250 cc. of 80 percent alcohol for 72 hours at 37° C. After driving off the alcohol and hydrolyzing with hydrochloric acid by heating to 76°, quantitative tests were made for reducing sugar as shown in table 12.

TABLE 12. *Acer saccharum. Sugars from xylem soluble in 80% alcohol. Hydrolyzed extract made up to 100 cc. 30 cc. samples tested from between rings and above, 25 cc. samples from the others*

	Dry Weight of Xylem Extracted	Individual Determinations Expressed as Mg. Invert Sugar			Average of Determinations	Mg. Invert Sugar Calculated for 25 Gms. Dry Wood
Above upper ring	23.33	14.15	14.66	14.58	14.46	53.91
Between rings........	31.78	59.6	59.85	59.05	59.5	155.84
Below lower ring.....	44.10	55.55	54.38	—	54.965	124.65
Check...............	37.07	40.08	39.10	—	39.59	106.80

From the data shown in table 12 it is evident that the removal of soluble carbohydrates from between two rings does not occur or is very much retarded. The carbohydrates above the upper ring were very much reduced. It is probable that, if a smaller stem had been ringed, the sugar content

above the ring would have been very much less; for in such cases shoot growth is quickly checked while in the present instance the shoot growth was apparently no less than in the check. The sugar content below the lower ring was less than that between the rings, showing that from this region some of the carbohydrates had been carried backward to the trunk whence they were carried towards the roots or to branches higher up. The unringed branch showed a sugar content higher than that above the ring and lower than that between upper rings, or below the lower ring. as would be expected.

After the removal of the soluble carbohydrates the residue was treated according to the Sachs method to determine the starch content. The material was boiled for two and one half hours under a reflux condenser in a flask with 10 percent hydrochloric acid of 1.9 specific gravity. The data obtained are recorded in table 13.

TABLE 13. *Acer saccharum. Polysaccharides from xylem hydrolyzed by Sachs method. Extracts made up to 500 cc., 25 cc. of this diluted to 200 cc. and 50 cc. samples analyzed*

	Dry Weight of Xylem	Mg. of Sugar Expressed as Glucose		Average of Determinations	Mg. of Glucose per 25 Gms. Dry Wood
Above upper ring	23.33	49.88	49.02	49.45	4,429
Between rings	31.78	73.00	72.55	72.775	4,580

The data indicate that there are more polysaccharides present in the stem between the rings than above, an equivalent of 151 milligrams of glucose. It is very evident, however, that by this method of extraction much material of the wood that is not starch is hydrolyzed. The iodine test showed only very faint traces of starch above the rings, yet by this method it would seem that this part of the stem contained starch to the extent of about 17.1 percent of the dry weight. It is very probable that pentosanes and possibly other polysaccharides were hydrolyzed.

TABLE 14. *Acer saccharum. Sugars from wood soluble in 95% alcohol. Extract made up to 100 cc., 25 cc. samples taken*

	Determinations Expressed as Mg. of Invert Sugar		Average of Determinations	Total Mg. Soluble Sugar Calculated for 25 Gm. Dry Matter
Above upper ring	12.1	11.8	11.45	45.80
Between rings	31.35	31.35	31.35	125.40

A second set of samples was extracted after a somewhat different manner. Pieces of xylem were sawed more finely into sections about one millimeter thick. Twenty-five gram samples of this dry material, including the sawdust produced in the process, were placed in 250 cc. of 95 percent alcohol and boiled for three hours in a flask with a reflux condenser. The solution was filtered off and the residue was extracted in the same way in fresh alcohol

second three hours. The filtrate was then freed of alcohol, hydrolyzed 10 percent hydrochloric acid for three minutes and tested for reducing The results are recorded in table 14.

evidently somewhat less sugar was extracted in this way than was cted in 80 percent alcohol. The ratio of the sugar content between to that above, however, is nearly the same in both determinations. e are respectively 2.74 to 1 and 2.89 to 1. The alcohol was removed from the residue by heating under vacuum. Water (300 cc.) was added and the whole was heated to 80°, cooled, and 0.2 gms. taka diastase added. At the time the diastase was added, the filtrate from the wood between rings showed a distinct blue with iodine while the other showed none. After standing 12 hours with taka diastase, 50 cc. samples of each were taken, hydrolyzed 3 minutes with 10 percent HCl and tested for reducing sugar. Calculated as glucose, the sample from between the rings contained 68.05 mg. of sugar and that from above the rings 26.24 mg. The total volumes of solutions were not exactly equal, so that these samples are not strictly comparable. The remainder of the solution was boiled for 3 minutes with 10 percent HCl in contact with the residue. The solution was filtered off, neutralized, and tested for reducing sugar. This is expressed in table 15 as glucose, but it is probable that some maltose remains.

TABLE 15. *Acer saccharum. Sugar obtained from residue by treatment with diastase and acid after removal of sugars soluble in 95% alcohol. Extract made up to 500 cc., 50 cc. samples taken*

	Individual Determinations		Average	Total in 500 cc.	Removed Before Treatment of Residue with Acid	Total for 25 Gms. Dry Wood Expressed as Glucose
Above rings........	51.9	51.95	51.925	207.70	26.24	233.94
Between rings........	92.25	93.08	92.665	370.66	68.50	439.16

A number of stems of *Fagus grandiflora* were double-ringed and results very similar to those described for Acer were obtained. All the stems tested with iodine showed a large amount of starch between rings and little or no starch above the upper ring. One experiment for which sugar analyses were made will be reported in detail. A young sapling was ringed 10 cm. from the ground and a second ring was made 70 cm. above the first. At this point the diameter of the stem was 30 mm. The rings were about 3 cm. broad. The ringing was done April 7, and the tree, with the check standing within three feet of it, was cut May 27. At this time the shoots had evidently completed their growth, but there was no apparent difference in the growth of the new shoots.

The tests for starch were as follows:

Above upper ring: No starch was present except in a very few scattered pith cells.

Between rings: Starch was very abundant in medullary rays and pi⸱ ⸱.

Below lower ring: There were distinct traces of starch in the medu ¦ary rays and in a few pith cells.

Lower part of upper ring appeared the same as between rings.

Upper part of upper ring: Starch was fairly abundant but distinctly less abundant than in the lower part.

Lower part of lower ring: Starch was fairly abundant in medullary rays and pith but less in the latter than between the rings.

Upper part of lower ring: The starch content was the same as between the rings.

Check: Traces of starch were present in smaller medullary rays and in the pith but less than just below the lower ring. This was true for all parts corresponding to those tested as described above.

The stems were cut into pieces 12 cm. long, from which all tissues outside the cambium were removed. These pieces were centrifuged, and the sap was tested for invert sugar after hydrolyzing with hydrochloric acid. The exact amount of sap remaining after removing 4 cc. samples was not determined as the tubes were rinsed out with water.

TABLE 16. *Fagus grandiflora. Sugar obtained from centrifuged stems*

	Green Weight of Sticks	Mg. Invert Sugar in 4 Cc. Samples	Mg. Invert Sugar in Remaining Sap	Total Invert Sugar Obtained.	Total Mg. Invert Sugar from Centrifuged Sap per 100 Gms. of Xylem
Check................	125.0	2.03	1.08	3.11	2.49
Above ring..........	185.4	1.25	0.72	1.97	1.06
Between rings........	219.6	1.67	3.76	5.43	2.47

The amounts of sap obtained were so small that the analyses cannot be fully depended upon, yet there seems to be clear indication that more sugar is present in the sap centrifuged from the xylem between the rings than from that above.

TABLE 17. *Fagus grandiflora. Sugar soluble in 80% alcohol hydrolyzed and expressed as invert sugar*

	Mg. Invert Sugar in 25 Cc. Samples		Average	Total Mg. Invert Sugar in the 50 Gms. Dry Wood
Check....................	42.34	43.7	43.02	344.16
Above rings..............	42.30	41.35	41.825	334.60
Between rings.............	61.08	60.20	60.64	485.12

The wood was sawed into short sections about a millimeter in length. After drying in the oven, lots of fifty grams each of this material, including the sawdust, were extracted in 250 cc. of 80 percent alcohol at 37° for 24 hours, and again in fresh alcohol for 72 hours. After heating to 80° the

on was filtered off, the alcohol was removed by repeated evaporation, he solution was finally boiled for 3 minutes with 10 percent hydroch- acid, neutralized, and made up to 200 cc.   The amounts of sugar found a hown in table 17.

he residues were shaken up with 250 cc. of water and 0.2 gm. taka d ase. After 12 hours the sawdust still contained abundant starch. T material was then placed in a steam autoclave at 15 pounds pressure for 45 minutes.   Two-cubic-centimeter samples diluted with 5 cc. of water and tested with iodine showed deep blue in the sample from between the rings and very faint traces of blue in those from the check and from above the rings. Five tenths of a gram of diastase was added to each and left 18 hours, but on examination starch was still present in the sawdust and in the small sections of wood. The material was then autoclaved a second time at 15 pounds for 10 minutes. On testing the extract as before, only that from between the rings clearly showed the presence of starch.

Without attempting to extract more of the starch, the solutions were filtered off and digested with 0.25 gm. of taka diastase.   Each of the extracts was then made up to 500 cc. and 25 cc. samples were tested for sugar.   This is expressed in the table as maltose, but it is very probable that much of it was really glucose.   Relative values, however, are all that are necessary.

TABLE 18.   *Fagus grandiflora.   Sugar obtained from residue by heating under pressure and digesting with diastase*

	Single Determinations Expressed as Maltose		Average	Total Sugar Present in 50 Gms. Dry Wood Expressed as Maltose
Check....................	46.03	40.24	43.14	862.80
Above rings...............	51.46	52.46	51.965	1039.30
Between rings.............	89.25	89.78	89.52	1790.40

DISCUSSION

The experiments with ringing accompanied by removal and non-removal of leaves clearly show that some substance necessary for growth passes upward through the phloem and that, if the leaves remain above a ring, they are able to supply some of this substance.   This substance may function as a food, supplying building material and energy, or it may function merely as an osmotically active agent, thereby enabling the tissue to compete successfully for water, or, as is more probable, it may function in both rôles.   Analyses show that ringing when leaves are removed results in a decrease both of osmotic pressure and of sugar content.   Removal of leaves without ringing also decreases the osmotic pressure and the sugar content below those of the normal stem with leaves.   The data obtained are not sufficient to enable one to determine with any degree of assurance whether sugar is the only or even the chief substance concerned.

The experiments with ringing dormant stems indicate that the gr wth above a ring practically ceases when the carbohydrates in this region are disappeared. Even the starch of the xylem itself is not digested an ! re. moved upward unless a path through the phloem is open. If that part above the ring is so short that the bud merely elongates but does not pen its leaves, growth ceases completely, and later the enlarged bud or partially opened leaves wither and die. If sufficient food was above the ring to enable one or two leaves to open, growth often slowly recommences, prob. ably because of the food made available by the new leaves.

The experiments with double ringing show even more clearly that the xylem does not serve as a tissue for longitudinal translocation of the car. bohydrates stored in it, for between rings the content both of starch and of soluble sugars is much higher than either above or below the part thus iso. lated. It would seem that the removal of carbohydrates from the xylem occurs only radially through the medullary rays and that longitudinal transfer in either direction is through the phloem only. In a ring 1 cm. wide starch was still present when all the starch had disappeared imme. diately above the ring. Later, however, the upper part had become de. pleted while the lower part was still full. Diffusion may have accounted largely for the movement through this short distance. Observation on this point has not been made, but it seems probable that much of the food from between rings will be eventually used up in cambial growth.

As was previously stated, Atkins (1916), finding appreciable quantities of sugars in the sap centrifuged from the stems of various woody plants, concluded that these must move upward with the "transpiration stream" and that one of the principal functions of the xylem is to transfer these sugars. The data here recorded, however, show that no appreciable amounts of sugar are transferred vertically through the xylem. In the experiments in which the leaves were removed above a ring, it seems possible that the lack of rapid transpiration might partly account for the failure of the xylem to transfer food; however, in the experiments in which dormant wood was ringed some distance from the tip plenty of leaves were produced above the ring to carry on rapid transpiration, yet this seemed to have no effect in causing the removal of either starch or soluble sugar below the ring, or from between rings in those stems that were double-ringed. In the the maple reported in tables 12–15, and in the beech reported in tables 16–18, there was a very large leaf surface that must have required quantities of water, but even the soluble sugars were not removed from between rings.

It will be necessary to make further tests on centrifuging the xylem before definite conclusions can be safely drawn, but the little that has been done at least suggests that even the sugar in the vessels does not normally move with the water in transpiration. We know that when a tree, such as the maple, is tapped, sugar solution will flow through the vessels. This is not proof, however, that in an uninjured tree there is any flow of solution through

. .ssels. If this were true, one would expect a depletion of carbohydrates
. . a ring in the maple, especially when it is ringed during the season of
. . ow and when the ring is only one to two centimeters broad.

. . possible frequent interposition of living cells across conducting tubes
. . readily prevent a flow of solution, and the water may normally move
. . . ly by diffusion. When a tissue is cut, however, as in pruning or in
. . ing, there is probably an actual flow of solution through the opened
. . els which might also result in a depletion of storage materials from adja-
. . t tissues. The movement of water through uninjured xylem may
. . ur chiefly by diffusion as in the case of the entrance of water from the
. . into a root. In the latter case there is certainly no flow of solution, as
the amount of water taken up has no relation to the amount of solutes
absorbed. Data reported by Kiesselbach (1916), who grew plants in soil,
indicate that increased transpiration does not increase ash absorption.
Experiments by the writer in collaboration with Dr. E. Artschwager and
Dr. N. B. Mendiola, that are nearly ready for publication, show that
doubling the transpiration from plants growing with their roots in nutrient
solutions has no tendency to increase salt absorption.

It may even be that at least some of the mineral nutrients move pri-
marily through the phloem. It is true that, if a stem is placed in a solution
of dye, the dye will rise rapidly through the xylem, but whether it will do so
in a normally rooted plant has not been conclusively proven. The writer
has found, however, that lithium chloride applied to a rooted plant will
move through the xylem past a ring. It is possible, however, that it was
not carried in the "transpiration stream" but rather that it moved past
the ring by diffusion. Lithium salts will diffuse much more rapidly than
sugars, and cell·membranes seem to be very permeable to them. [The
lithium was found in the phloem and cortex above the ring as well as in the
xylem.

A number of papers have been published in which it has been shown that
certain dyes or salts appear to travel in the "transpiration stream" through
the xylem when the roots of the plant are placed in the solutions. But in
many cases the dyes or salts used may have had toxic effects as a result of
which the cells that might normally retard their movement may have been
killed or their permeability may have been increased. Furthermore, it
has been found in a number of instances that the solutes appeared to travel
at about the same rate in the phloem region as in the xylem. Bokorny
(1890) found that, when roots were placed in solutions of iron sulphate or
of various dyes and the leaves were exposed to very drying conditions, the
solutes were found in the phloem region at about the same height as in
the xylem region. When on the other hand a cut stem was placed in the
solution, the movement through the xylem was distinctly the more rapid.
Because he always found the solutes not in the lumina but in the walls of the
thicker-walled elements, such as the vessels, sclerenchyma, and collenchyma
cells, Bokorny came to the conclusion, which has since been clearly dis-

proved, that water moves through the walls by imbibition. Though his conclusions are of little value, his data at least suggest that solutes are not necessarily carried by the "transpiration stream."

It will be necessary to conduct experiments using rooted plants and various non-toxic salt solutions before any very definite conclusions can be drawn as to the region of transfer of salts in plants.

SUMMARY

Defoliated stems from which a ring of tissue extending to the cambium is removed cease to continue growth.

This cessation is due to the inability of the xylem to carry the necessary food.

This food is needed not only to supply energy and building material but also to increase the osmotic concentration of the tissues, thereby enabling them to absorb water.

This food consists, at least partially, of carbohydrates.

If the stem above a ring is not defoliated, the leaves are able to supply sufficient of this food to allow for considerable growth.

When dormant stems are ringed, the growth above the rings ceases soon after the starch supply is depleted, and the greater the supply of starch above a ring the longer will growth continue.

The carbohydrates stored in the xylem below the ring can not be removed through the xylem but must be transferred radially to the phloem, where they may be carried downward if there is no second ring below.

The carbohydrates of the xylem between two rings remain there at least for some time after those above the upper ring and those below the lower ring have been mostly removed.

Although large amounts of carbohydrates are stored in xylem tissues, there is no appreciable longitudinal transfer of sugars through these tissues.

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